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AGENCIES WHICH GOVERN THE DISTRIBUTION OF LIFE

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THE problems presented by the distribution of plants and animals is a fertile field for investigation. These problems are essentially ecological in character, for often, perhaps always, the range of a species or genus is dependent upon a number of diverse environmental factors, some of which are readily apparent, while others are obscure; but always they merit careful study.

In investigating and mapping the ranges of living organisms and in following the evolutional tendencies of species in so far as we are able, environment and its influences are of the greatest moment, especially from an ecological standpoint. Botanical subjects may usually be allocated in relation to their surroundings with considerably greater ease than can active forms of life, for the former are acted upon only by the agencies to be found in one spot, while the latter may experience not only all the influences operative over several square miles, more or less, of diversified territory, but, in the case of a migratory bird or mammal, will be subject during a part of the year to environmental factors of which we may know nothing. Whether a species is common or rare in a certain area depends upon its rate of reproduction, which is usually entirely adequate unless new and disturbing influences have been introduced; upon the number of favorable or unfavorable conditions which it encounters, the amount of competition with which it has to contend, and its phylogenetic characters, as to whether it be of a plastic type or one which is senescent and overspecialized: all of which may be summed up in the phrase "adaptability to its habitat."

In any one realm, or larger region of the earth's surface, there are various climatic divisions, the chief of which have been named zones, and these stretch across the continent following isotherms, or mean temperature bands, usually, for our purpose, based upon the average amount of heat present during the three chief reproductive months. Zones are divisible into faunal districts, whose bounds are limited by conditions of humidity, precipitation and a few other causes that may be operative over considerable areas. These are further divisible into associations, an almost limitless number of which may be recognized. Thus, we have littoral, riparian or stream bank, palustral or marshy associations, the latter being capable of still narrower subdivision into tule, arrow-head or salt grass associations, and so on without end.

Associations are sometimes but little considered in parts of the country where climatic conditions are uniform over a wide extent of territory; but in the mountainous parts of the west, where practically every possible local environment from the hottest, most arid deserts, to arctic-alpine conditions may be encountered within a few miles, the importance of their recognition can hardly be overestimated.

In considering the agencies governing the range of a form, the question of temperature is undoubtedly of chief importance as a usual thing, but in some cases physical barriers should be given greater weight, for it need hardly be indicated that it is such directly—and temperature only indirectly if at all—that keep many forms of life from greatly increasing their ranges. In studying such barriers, manner of dispersal may be of much importance. In the case of plants more than of vertebrates (with few exceptions), human agency must now be taken into account, for the activities of man, both intentional and unintentional, are responsible in greater degree for the widespread dissemination of seeds and insects over vast stretches of the earth's surface than any other cause. Natural manner of dispersal must also be carefully scrutinized as a preliminary step, for what will prove a barrier to the extension of the range of a plant with what I may term unadorned seeds may be inoperative in the case of seeds adapted to dispersal by the wind, and again, those whose covering is fitted for adhesion to the coats of mammals will often be still more widely scattered.

In the case of an animal, the first thing to be considered is the life-type to which it belongs, the chief divisions of which are aquatic, fossorial, terrestrial, arboreal and volant types, which are limited in varying degrees by physical barriers. To an aquatic form, land masses are insuperable obstacles, while to many terrestrial species, especially such as live in very arid regions and are totally independent of water, even a large river may prove a delimiting agent. A strip of rocky country or an extent of arid plain will prevent the spread of such a fossorial mammal as the mole. Arboreal forms are checked by large, treeless areas, and animals which are adapted to a life on the plains will usually shun the forests. Volant types are the most independent of physical barriers of all, and to some even wide stretches of ocean are no obstacle, as in the case of the Pacific Golden Plover (*Charadrius dominicus fulvus*), in its annual migrations between Alaska and the Hawaiian Islands.

While conceding that temperature is the most important factor in the distribution of life, the writer is of the opinion that not enough importance has been credited to other agencies. Dr. C. H. Merriam was, I believe, the first to formulate the theory that the northward range of a species is governed by the mean amount of heat present during the season of reproduction, while the southward range of northern forms is restricted by the mean temperature during the very hottest portion of the year. Isotherms have been determined and our continent plotted and mapped into zones, called Arctic, Hudsonian, Canadian, Transition, Upper Sonoran, Lower

Sonoran and Tropical, some of which are known by other terms in the eastern part of the country. Roughly, the position of an isotherm, as well as the temperature of a region at other times of the year, depends upon latitude, altitude and distance from the sea. Hence it is that the winter temperature of parts of Montana at a considerable altitude and far from the sea reaches a lower figure than has been recorded on the coasts of the Arctic Ocean. The coldest temperature ever known upon the face of the earth—minus 92 degrees F. in the interior of Siberia—is much lower than has ever been found by any of the "farthest north" expeditions.

We may safely infer that the degree of winter cold, below a certain point, is largely immaterial, for it makes no difference to a tree whether the thermometer is ten or sixty degrees below zero, nor to the lesser vegetation and many rodents safely protected by a deep blanket of snow. Even to the few species of birds which habitually spend the winter in high latitudes, very low temperatures are seldom disastrous, but rather is it due, when numbers perish, to a failure of the food supply during sleet storms or long blizzards. Neither birds nor mammals migrate so much because of cold as because their usual foods are not to be obtained in adequate amounts during the winter.

Certain forms of life may have to contend, in relatively low latitudes and altitudes, with conditions which approximate those to be found much farther north. W. T. Shaw has but just brought to our attention the fact that in eastern Washington, where Upper Sonoran conditions are the rule, estivation and hibernation of the Townsend Ground Squirrel (*Citellus townsendi*) are so long continued that this animal enjoys but four months of activity during the year. The squirrels emerge as soon as the first growth starts in the spring, but retire to their burrows for the long sleep when the arid conditions of early summer cause a desiccation of their food supply. To a torpid animal in its nest below ground it makes no difference whether it is summer or winter above, and so these squirrels seem to lead an existence closely similar to that of their near kin at the Arctic Circle, but with the probable difference that the northern forms experience an actually greater number of hours of daylight throughout the long arctic summer months.

In the plains section of the interior, zonal divisions are acted upon by comparatively few modifying agencies, and their boundaries are rather regular and easily defined, but in parts of the three Pacific Coast states, whose shores are bathed by warm ocean currents, and where the topography is decidedly irregular, the problem of zonal definition is often extremely complicated. In the coast region of northern California, for instance, there is but slight daily and seasonal change of temperature, and a number of Boreal forms are able to occur there because the summers are cool enough for them, while certain Sonoran species are also able to exist because the mean temperature of the breeding season is high enough for their needs. The result is a confusion of zonal indices that is extremely puzzling at first glance.

To these three widely-recognized zonal factors, when operative in certain regions, should undoubtedly be added character of the coastal sea currents—whether warm or cold—and direction of the prevailing winds.

Faunal conditions depend largely upon humidity as well as upon all zonal factors. The chief cause of a humid climate is, of course, ample precipitation, either rather evenly distributed throughout the year, or else supplemented during the drier season by heavy fogs and dense forests to retard evaporation, while a cool climate is often helpful. Precipitation may be largely dependent upon the position of adjacent mountain masses with respect to the prevailing winds, for, as is well known, moisture-laden air is cooled upon contact with an elevated land mass, and precipitation results; but little moisture will then be left in the clouds for rain in the trans-montanic sections. This fact is beautifully shown by the humid and heavily forested coast and mountain areas of northwestern Washington, in contrast to the bare, arid plains east of the Cascade range.

Associational temperature is induced by many causes, and although limited in extent it profoundly influences local zonal boundaries. Even associational factors other than temperature may raise barriers to distribution that are insurmountable to many organisms.

Insolation, or the relative amounts of sun and shade received by a species in its habitat, is sometimes of paramount importance. This may be influenced by cloudiness, by the amount and density of surrounding vegetation or by the character of the topographical environment. In illustrating this point, we may mention as extremes the bottom of a deep, narrow, forested gulch, and the top of a warm, bare ridge; the face of a steep north slope, and one facing south. A gully on a north slope may be so situated as never to receive the rays of the sun, while at a certain optimum angle one facing towards the south will receive forty per cent. more solar heat than will a level surface. Hence, zonal boundaries upon the two slope aspects will be found to occur at very different altitudes. Soil conditions are of great importance in influencing the temperature immediately above its surface, and its character helps to control both the amount of evaporation and the degree of moisture which it is capable of retaining. A light-colored soil is considerably cooler, other things being equal, than a dark, rocky one, which will absorb and retain more heat. The importance of the chemical composition as well as the mechanical condition, with amount of humus, acid or alkali, in the soil need be no more than mentioned.

The temperature of the soil and the atmosphere above it is often greatly influenced by near-by cold mountain streams, and in places zonal boundaries may be depressed one or two thousand feet in altitude by this agency. Large snowbanks and glaciers have a similar effect, though usually less pronounced or, rather, more locally restricted. A forest fire or avalanche, by destroying ground shade with the consequent raising of the soil temperature, will usually cause an area to grow up to plants and trees of the zone immediately below, to be gradually restored, in future years, to its original zonal status. Base level has its effect, for the foot of a mountain mass rising from a plain five thousand feet in altitude will have lower zonal tendencies than will the five thousand foot level of a mountain rising from a plain with an elevation of but one thousand feet, because the higher plain accumulates more heat. Similarly, a large mountain mass is less influenced by the conditions which surround it than is an isolated peak. A steep slope will carry a certain zone to a greater height than will a gentle one, because the former will receive, during the day, more of the warm air arising from the lowlands, and the cold air which descends during the night will flow off more rapidly. However, this rule is often nullified by the steep slope being so situated that it receives less sunlight than the more gentle gradient. These points are finely illustrated on most of the mountains of the southwest. Plants and trees of the Transition Zone often flourish on the bottom of a north-facing canyon, while the Sonoran sagebrush extends a couple of thousand feet higher upon the steep slopes with southern exposures.

Protective cover is important to most of the more retiring forms of active life, and to such it is not only necessary as a screen during their daily foragings, but they must have holes into which they may dart at the approach of danger and safe retreats in which to rear their young. To very few vertebrates is the actual character of the soil of great moment, but there are exceptions, as instanced by the large kangaroo rat, *Dipodomys deserti,* the front feet of which are so weak that it seems able to burrow only in deposits of æolian or other loose sand, and it is useless to expect to find this species in hard soil. Needless to say, character of food, both general and specific, is a powerful determining factor of distribution, and with this should be classed not only the manner of feeding but the methods employed in securing sustenance. The search for a favorite food item will even, in time, indirectly change a mammal from a terrestrial to an arboreal type, as it evidently has the tree mouse, *Phenacomys longicaudus,* of the coasts of Oregon and northern California, which, so far as known, feeds exclusively upon the needles of coniferous trees.

The question of enemies, it seems to me, should be given much more weight in distributional problems than it usually receives. This factor may be divided into active and passive enemies. By the latter term is meant competitive forms, as the more robust growth that chokes out a tender seedling, or an organism which, being more adaptable to a variety of conditions, forges ahead of less plastic forms whose habits are competitive. It is the opinion of the writer that such competition constitutes the real remorseless struggle for existence which most species are obliged to carry on in order to survive, rather than their efforts to elude their active enemies. Although these passive enemies are not spectacular and are apparent only after scrutiny by an understanding person, they are, nevertheless, always present and operative.

Active enemies may be divided into irritating and exterminating types, and in certain sections the former may constitute a formidable barrier to dispersal. Few of the larger parasites directly cause death, but the presence of great quantities of aphis, scales, ticks or intestinal worms upon their respective hosts may so handicap a species that it is forced to the wall by the competition of more favored forms. Unusual numbers of horse flies in a mountainous section may so harass stock that they utterly refuse to dwell in such regions.

Exterminating agencies may consist of directly predaceous organisms, such as carnivores which consume the flesh of their victims, or rodents whose presence in great numbers seriously interferes with the propagation of certain plants. The overstocking of a range with cattle or the presence of a vast colony of prairie dogs may actually extirpate certain grasses in those districts, and hordes of some rodents will prevent reforestation in spots because all tree seeds are eaten as fast as produced. Poisonous plants work great havoc among range stock at times, and although the amount of such devastation among wild forms has seldom or never been investigated, it is doubtless an appreciable factor. In some regions, bacteria and disease, including the smaller parasites, play a most important rôle. The tse-tse fly in portions of Africa has rendered it utterly impossible for certain herbivorous mammals to be kept in the infested districts; the *Stegomyia* mosquito that is instrumental in the spread of yellow fever probably caused the Mayan survivors of this dread disease to abandon the ancient civilization of Yucatan, which was at one time so densely populated, and many ailments, comparatively harmless to white men, who have developed a degree of immunity to them, are largely responsible for the decrease in the numbers within recent years of the more savage peoples. From time to time either totally new bacterial diseases appear or else old ones suddenly acquire new virulence, and throughout the ages, such have undoubtedly killed off certain species from faunal divisions; and it is not at all improbable that during the course of bacterial evolution whole genera, or even families, have been exterminated by this agency.

It seems advisable to append to the present paper a chart, or key, to the factors chiefly responsible for the distribution and restriction of the ranges of living forms, but this is submitted with considerable hesitancy. Most of the factors mentioned are so interdependent upon others that it is merely a matter of personal opinion as to which heading they should be placed under. For instance, it is impossible to decide whether the effect of a cold mountain stream should better be listed under zonal or associational conditions, for it is operative in both connections. It should be understood, therefore, that the arrangement is only tentative, and that the list has been made to conform to the viewpoint of a vertebrate zoologist.

FACTORS TO BE CONSIDERED IN THE DISPERSAL OF LIFE

Life Types:
- Active Forms.
  - Aquatic.
  - Fossorial.
  - Terrestrial.
  - Arboreal.
  - Volant.
- Sedentary Forms.
  - Character of Habitat.
    - Manner of seeding or reproducing.

Direct Physical Barriers:
- Oceans, rivers, etc. (to land forms).
- Land masses, mountains, etc. (to aquatic forms).
  - Forests, plains, deserts, etc.
    - Protective cover.

Regulation by Temperature:
- Zonal

Latitude. Altitude. Proximity to sea. Ocean currents. Prevailing winds.	Mean temperature during reproduction. Mean maximum. Mean minimum. Delimiting temperatures (as frost to tender species).

- Faunal.
  - Humidity.
    - Precipitation.
      - Location of near mountain masses, if any.
      - Location of near bodies of water, if any.
- Associational.
  - Degree of insolation.
  - Effects of fires and avalanches.
  - Presence of cold streams or glaciers.
  - Topographical situation.
    - Slope aspect.
    - Slope angle.
    - Base level.
  - Soil.
    - Chemical and mechanical character.

- Color.
- Moisture.

Food:

- General and specific character.
- Feeding habits.

Enemies:

- Passive (competitive forms).
- Active.
    - Irritating.
    - Exterminating.
        - Directly predaceous.
        - Poisonous foods.
        - Bacteria, protozoa, etc.

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